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AN EVALUATION OF NINE BACKCROSS-DERIVED WHEATS¹

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THE IMPROVEMENT of established varieties of wheat through use of the backcross method of breeding was pioneered at the California Agricultural Experiment Station (Briggs, 1930).³ It seems advisable to present a new appraisal of the method that is based upon recent progress. For the plant breeder, the farmer, and the miller, the principal concern involves the degree of similarity, or difference, between a known commercial variety and its improved successor evolved by backcrossing where injury from diseases and insects does not occur. The results of numerous comparisons under such conditions are presented here. The procedures followed in the breeding of nine improved varieties and the genetic nature of these varieties are also discussed.

REVIEW OF LITERATURE

Theoretical assumptions regarding homozygosity of backcrossed populations and their similarity to their prototype varieties have been presented by Briggs (1930, 1938). These assumptions furnished the justification for the release of the improved varieties for commercial culture before extensive comparative performance data were available. Subsequently, a series of reports, each treating a successively larger body of data have been presented (Briggs, 1938; Suneson and Briggs, 1941; Suneson, Riddle, and Briggs, 1941; Riddle and Baker, 1944) emphasizing the similarity between the improved varieties and their prototypes. The improved varieties have been widely accepted by California farmers because of the economic advantage of the obvious improvements. In 1939, Baart and White Federation occupied 56 per cent of the California wheat acreage (Clark, 1942). In 1944, however, Baart 38 and White Federation 38, together with a very small residue of their prototypes, occupied approximately 70 per cent of the California wheat acreage, according to all available reports. This trend had been predicted (Suneson, 1945), but it was accelerated by state-wide rust damage in 1940 and 1941.

¹ Compiled from investigations of the Division of Cereal Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Dept. of Agriculture; and the agricultural experiment stations of Arizona, California, Colorado, Idaho, Montana, Oregon, Washington, and Utah cooperating in a regional wheat-improvement program.

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³ See "Literature Cited" for citations, which are referred to in the text by author and date.

MATERIALS AND METHODS

Since the results given in this paper are practical attempts to show the degree of return to the recurrent parental type in California backcross-derived varieties, special interest attaches to the pedigrees of the several improved varieties. The number of backcrosses and the size and management of the successive backcross generations are especially important. The pertinent facts are given below.

Big Club 37, C.I. No. 11901: Big Club 37 was derived from Martin backcrossed to Big Club six times (Martin \times Big Club⁷). The first cross was made in 1922 and six backcrosses were added and successively tested for bunt, generally on F₃ strains in alternate generations of backcrossing, until 1936, when 77 homozygous bunt-resistant F₃ lines were bulked to make the variety.

Sonora 37, C.I. 11902 (Martin \times Sonora⁷): Sonora 37 was produced in the same way and at the same time, 71 F₃ lines being bulked.

Pacific Bluestem 37, C.I. 11903 (Martin \times Pacific Bluestem⁷): This variety, also produced at the same time and in the same way, consists of a composite of 78 F₃ lines.

White Federation 38, C.I. 11906 (Hope-White Federation⁵ \times Martin-White Federation⁶): Martin smut resistance and Hope stem-rust resistance carried through independent backcrossing programs and then merged in a final cross from which 182 doubly resistant F₃ lines were bulked in 1937.

Baart 38, C.I. 11907 (Hope-Baart⁵ \times Martin-Baart⁷): This variety was produced in the same way and at the same time as White Federation 38, except that 157 F₃ lines were bulked.

Onas 41, C.I. 12,229 (Martin-White Federation³ \times Onas⁶): Onas 41 is a composite of 115 homozygous bunt-resistant F₃ lines.

Federation 41, C.I. 12,230 (Martin-White Federation³ \times Federation⁶): Federation 41 was produced concurrently with Onas 41 from a composite of 130 F₃ lines.

Poso 42, C.I. 12,237 (Dawson \times Poso⁶): This Hessian-fly-resistant variety is a composite of 45 F₄ lines.

Big Club 43, C. I. 12,244: This variety is a composite of 144 triply resistant (bunt, Hessian fly, and stem rust) F₃ lines. It resulted from three independent breeding programs:

(1) Production of Big Club 37 as noted above.

(2) Dawson-Big Club⁴ \times Big Club 37².

(3) Hope-Baart⁴ \times Big Club² \times Big Club 37².

The final merger involved random crossing of (2) on (3), and then of (2) on the F₁ of these.

Comparisons herein reported are drawn from plot or nursery tests in which the commercial variety and the improved strain were grown in paired tests, where stem rust, bunt, or Hessian fly was not reported as a differentiating yield factor. Most of the data were compiled from results at 18 experiment stations coöperating in the western regional wheat-improvement program (Suneson, Riddle, and Briggs, 1941). Other data came from coöperative tests on farms in California and Nevada. Yield data are reported for individual plots, while other data, such as height, heading date, test weight, and lodging

are reported only as an average for the several replicates (either an average of independent measurements, or a single measurement on a composite sample). All available data on each item are included.

TABLE 1

COMPARATIVE YIELDS OF BAART AND BAART 38 AT WESTERN EXPERIMENT STATIONS AND IN CALIFORNIA AND NEVADA FARM TESTS, 1939-1944*

Station	Mean yields per acre		Yield differences	Binomial yield distributions		
	Baart	Baart 38		Number of times superior		Number of ties
				Baart	Baart 38	
	<i>bushels</i>	<i>bushels</i>	<i>bushels</i>			
California.....	35.9	36.6	+0.7	31	32	4
Nevada farms.....	29.1	29.9	+0.8	5	4	0
Mesa, Ariz.....	38.8	39.3	+0.5	4	6	0
Sacaton, Ariz.....	30.6	31.0	+0.4	1	2	0
Hesperus, Colo.....	44.8	42.0	-2.8	3	2	1
Pendleton, Ore.....	37.4	35.8	-1.6	11	7	0
Moro, Ore.....	26.4	26.7	+0.3	16	14	0
Union, Ore.....	54.2	55.3	+1.1	7	4	0
Pullman, Wash.....	52.1	52.8	+0.7	9	13	2
Prosser, Wash.....	49.9	48.4	-1.5	7	4	1
Lind, Wash.....	25.1	25.3	+0.2	7	10	1
Pomeroy, Wash.....	28.0	28.4	+0.4	5	4	2
Walla Walla, Wash.....	38.3	38.4	+0.1	9	9	0
Moscow, Idaho.....	37.2	36.6	-0.6	6	12	0
Sandpoint, Idaho.....	24.8	24.6	-0.2	2	3	0
Tetonia, Idaho.....	28.4	25.1	-3.3†	16	6	0
Aberdeen, Idaho.....	68.4	68.6	+0.2	12	8	0
Bozeman, Mont.....	58.6	57.3	-1.3	9	5	0
Logan, Utah.....	54.2	54.9	+0.7	7	6	0
All tests.....	39.59	39.45	-0.14	167	151	11

* This summarizes all cooperative plot and nursery tests reported to the author excluding only nonpaired tests, or tests wherein stem rust affected yields. The California tests include tests on farms in cooperation with the Agricultural Extension Service.

† Odds are greater than 19:1 that this difference is not due to chance.

Mean differences, supported by odds determined from the point binomial distributions (Miles, 1935) are used to determine the similarity between the commercial and the improved strain. This method of statistical analysis is conservative and is particularly useful in studies of this kind because of its ease of application.

RESULTS

Agronomic Evaluation. Since Baart was the most widely grown variety in the western region (Clark, 1942) and Baart 38 has now almost completely replaced it in California, Arizona, and Nevada and is being grown in Oregon,

Idaho, and Utah, it is logical that the most extensive comparisons involve these two varieties. Detailed data on yield from all available sources in the region are presented in table 1. These represent tests from 1939 through 1944, excluding only nonpaired tests or comparisons in which stem rust was a differentiating yield factor. For the six-year period, 59 tests were excluded because of the presence of stem rust. Mean yields of the two varieties at all locations and the number of times when each was superior are shown. From this it can be deduced that only at Tetonia, Idaho, has a significant difference (at the 5 per cent level) between the two varieties been found. In this case the results favored Baart.

TABLE 2
DIFFERENCES IN AGRONOMIC CHARACTERISTICS BETWEEN BAART AND BAART 38,
WESTERN REGIONAL TESTS*

Year	Date headed (April 16 to July 22)		Plant height (25 to 68 inches)		Lodging (0 to 25 per cent)		Weight per bushel (53.9 to 66.5 pounds)	
	Number of tests	Mean difference	Number of tests	Mean difference	Number of tests	Mean difference	Number of tests	Mean difference
		<i>days</i>		<i>inches</i>		<i>per cent</i>		<i>pounds</i>
1939.....	11	-0.1	11	-0.3	2	-9	13	+0.1
1940.....	10	+0.2	12	-0.3	6	+1	11	+0.3
1941.....	13	-0.8	12	-0.1	3	-2	4	+0.3
1942.....	11	0.0	12	-1.0	4	-6	12	+0.6
1943.....	10	+0.3	11	0.0	4	+5	11	+0.4
1944.....	10	+0.3	12	-0.5	5	-9	12	+0.3
Total or mean.....	65	-0.05	70	-0.36	24	-2.8	63	+0.33

* Exclusive of environments known to be favorable to the improved variety.

As an average of all 329 plot comparisons, no significant difference was found despite the wide range of environments in which the tests were conducted. This means that although Baart outyielded Baart 38 by an average of 0.14 bushel, there is little likelihood that there is any real difference between these two varieties.

Comparative agronomic data for Baart and Baart 38 are presented in table 2. It has been mentioned that the unit data treated here are available only as averages of all plots at each station. The fact that some stations have equipment for determining test weights that is calibrated in half-pound intervals, while others show 0.1 pound difference is also worthy of note. Nevertheless, the preponderance of individual instances in which Baart 38 was shorter and weighed more per bushel than Baart suggests that the small average differences reported are probably significant. The differences in height and in test weight were 0.36 inch and 0.33 pound per bushel, respectively. While Baart 38 showed a range of from 2 days earlier to 5 days later than Baart, its average heading date was the same as for Baart. Other differentiating agronomic comparisons failed to show significant differences between the two varieties. These comparisons are not shown in table 2, but such factors as shattering and susceptibility to mildew, septoria, stripe rust, and root rot are included.

In establishing some slight, but apparently significant differences between the two varieties, it must be remembered that they are nevertheless substantially alike—so much so that large populations and diverse environments must be sampled to establish the slight differences herein reported.

Apart from emphasizing similarities between Baart and Baart 38, it also seems desirable to call attention to the economic advantage resulting from the commercial distribution of Baart 38. Its resistance to certain races of bunt and stem rust is unquestioned. Comparative tests in the presence of bunt have not been conducted, but a fairly representative body of data from stem-rust environments is available. Of the 59 tests excluded from table 1, 23 were

TABLE 3

DIFFERENTIAL ANNUAL DEVELOPMENT OF STEM RUST ON BAART AND ON BAART 38 AT DAVIS,
WITH RELATED YIELD AND TEST-WEIGHT DATA

Test year*	Stem rust		Test weight		Acre yield	
	Baart per cent	Baart 38 per cent	Baart pounds	Baart 38 pounds	Baart bushels	Baart 38 bushels
1938.....	5	0	60.7	61.7	46.0	49.2
1939.....	10	tr	64.5	64.2	54.2	52.6
1940.....	30	0	62.2	63.1	48.8	53.7
1941a†.....	20	0	61.4	62.7	39.0	36.1
1941b†.....	60	tr	58.4	61.4	29.1	36.4
1943.....	60	tr	59.2	63.0	33.7	46.0
1944.....	30	3	62.1	61.7	47.5	58.5
Mean.....	31	1	61.2	62.5	42.6	47.5

* No stem rust developed in the 1942 tests.

† 1941a, seeded November 26, 1940; 1941b, seeded January 31, 1941.

in California and cover all years from 1938 to 1944 except 1942. None of these involved a susceptible stem-rust reaction in Baart 38, nor an extremely high incidence of stem rust in Baart. Nevertheless, the average of these California tests, in which there was 31 per cent of rust-damaged tissue in Baart and only 1 per cent in Baart 38, produced an average difference of 1.3 pounds in test weight and 5 bushels in yield, as shown in table 3. Although not all of the area in which Baart is grown in California is subject to as frequent or as severe an incidence of rust as was experienced at Davis from 1938 to 1944, some areas are far more vulnerable. Also the state-wide severe losses of 1940 and 1941 must not be overlooked. It is safe to assume an average annual yield advantage of 10 per cent for one fourth of the 160,000 acres of Baart 38 that is now being grown. Since rust is more common on fertile lands, the average yield of Baart is about 40 bushels per acre. On this basis, the release of Baart 38 has added 160,000 bushels annually to California's wheat production. This is accomplished without any change in wheat acreage or change in the basic varietal type. Furthermore, Baart 38 tests on the average 1.3 pounds more per bushel where rust occurs and also tests slightly more than Baart in other sections—an advantage to the miller. Similar annual yield increases and production security followed the release of White Federation 38, which also is grown on approximately 160,000 acres in California.

For the region as a whole, the occurrence of rust was less frequent than in California. In a few instances rust races appeared to which Baart 38 is nearly as susceptible as is Baart. Nevertheless, an average of all the 59 tests in which rust injury was recorded showed a bushel weight difference of 1.3 pounds, and a yield difference of 3.5 bushels in favor of Baart 38.

Eight other backcross-derived varieties have been compared with their commercial prototypes in 13 or more tests in which their resistance to rust, bunt, or Hessian-fly injury was of no advantage. These data are summarized in table 4. Four of these varieties were grown in additional states, but Sonora 37, Big Club 37, Poso 42, and Big Club 43 were tested only in California.

TABLE 4

COMPARISON OF YIELDS AND THEIR UNDERLYING BINOMIAL DISTRIBUTIONS FOR BASIC AND BACKCROSS-IMPROVED STOCKS OF WHEAT VARIETIES IN WESTERN REGIONAL TESTS*

Varieties compared	Comparative data			Analysis of differences			
	Number of comparisons	Mean yields per acre		Yield differences	Number of times superior in yield		Number of identical yields
		Prototype variety	Improved variety		Prototype variety	Improved variety	
Baart vs. Baart 38.....	329	<i>bushels</i> 39.59	<i>bushels</i> 39.45	<i>bushels</i> -0.14	167	151	11
White Federation vs. White Federation 38.....	217	38.27	38.58	+0.31	105	105	7
Onas vs. Onas 41.....	136	52.50	52.72	+0.13	69	64	3
Federation vs. Federation 41.....	137	50.70	50.41	- .29	68	64	5
Pacific Bluestem vs. Pacific Blue-stem 37.....	85	34.88	36.15	+1.27	38	43	4
Big Club vs. Big Club 37.....	44	38.54	37.30	-1.24	25	19	0
Sonora vs. Sonora 37.....	14	36.18	36.00	-0.18	7	5	2
Poso vs. Poso 42.....	16	33.06	32.64	-1.02	9	3	4
Big Club vs. Big Club 43.....	13	33.86	33.63	-0.23	6	7	0

* Exclusive of environments known to be favorable to the improved variety.

In no case has a significant mean yield difference between a commercial variety and its backcross-derived successor been established. Nonsignificant differences are either positive or negative, according to the variety comparison involved. Hence, it must be concluded that all pairs are substantially alike in their aggregate yield performance over a wide diversity of environments. The data were compiled by individual stations but regional averages only are reported here. At only one station—Aberdeen, Idaho—does the difference in yield appear to be significant. Federation, with an average yield of 82 bushels, exceeded Federation 41 by 4.4 bushels, being superior in 11 of the 13 comparisons. With this exception none of the differences in agronomic data appear to be significant.

Quality. Each season certain varieties under test in the western region are subjected to milling, baking, and other physical and chemical tests (Fifield, *et al.*, 1941). The averages of all such tests with experiment-station samples of the four principal variety pairs grown during the years 1938 to 1943 are shown in table 5. Some modifications in analytical procedure and baking formulas have occurred during the experiments, but for purposes of gross evaluation these have been disregarded in computing averages.

TABLE 5

QUALITY CHARACTERISTICS OF FOUR BACKCROSS-DERIVED VARIETIES AND THEIR COMPARABLY GROWN PROTOTYPES
(Based on averages from a number of locations in the western states during two or more years from 1939 to 1943)

Variety	Analysis of wheat				Analysis of flour								
	Station- years	Crop years	Acre yields	U. S. grade	Hard kernels	Test weight*	Flour yield†	Pro- tein†	Carot- enoid	Pearl- ing index	Dough- ball time	Pro- tein†	Ash†
	number	number	bu.		per cent	lbs.	per cent	per cent	p.p.m.	per cent	min.	per cent	per cent
Baart.....	42	6	48.8	1 H.Wh.	90.7	62.1	70.0	11.7	2.23	41.4	54	10.2	0.52
Baart 38.....	42	6	43.2	1 H.Wh.	90.5	62.5	70.6	11.9	2.22	40.8	60	10.5	0.54
White Federation.....	35	5	49.2	1 H.Wh.	88.8	61.2	71.3	11.1	2.48	32.1	150	10.2	0.51
White Federation 38.....	35	5	49.8	1 H.Wh.	89.1	60.8	71.3	11.4	2.37	32.9	159	10.5	0.50
Onas.....	14	2	54.6	1 S.Wh.	64.0	60.9	70.6	9.4	3.03	29.4	105	8.0	0.50
Onas 41.....	14	2	55.5	1 S.Wh.	62.5	60.9	71.3	9.5	3.03	30.2	111	8.3	0.51
Federation.....	14	2	52.5	1 S.Wh.	62.5	60.2	71.0	9.7	3.25	27.0	63	8.3	0.49
Federation 41.....	14	2	52.5	1 S.Wh.	70.5	60.6	71.7	9.9	3.37	27.8	68	8.5	0.45

Variety	Yellow loaf cake				Cooky test		Bread test									
	Volume	Grain and tex- ture	Crumb color	Sym- metry	Factor W/T‡	Color	Top grain	Absorp- tion	Loaf volume		Grain		Texture		Crumb color	
									For- mula 1¶	cc 2¶	For- mula 1¶	score 2¶	For- mula 1¶	score 2¶	For- mula 1¶	score 2¶
Baart.....	cc 950	score 103		G	ratio 4.93	B	G	per cent 53.7	cc 575	530	score 74	71	score 81	76	score 81	76
Baart 38.....	978	105	102	G	5.03	B	G	54.0	545	554	63	68	69	75	66	69
White Federation.....	905	86	96	F	4.51	LB	P	60.8	634	632	80	83	93	91	77	78
White Federation 38.....	893	81	93	F	4.48	LB	P	61.5	620	679	79	88	91	94	77	83
Onas.....	965	105	98	G+	5.99	B-	G+	54.0	481	535	63	70	55	68	65	75
Onas 41.....	928	105	98	G	5.65	B	G+	54.0	465	520	55	70	61	68	63	68
Federation.....	942	105	95	G	5.71	B	VG	54.0	478	521	58	63	61	68	53	65
Federation 41.....	983	103	95	G+	5.37	B-	VG	54.0	495	530	58	68	61	68	60	73

* Dockage free.

† Moisture free.

‡ Width divided by thickness.

¶ Formula 1 is the commercial formula; formula 2 is the same with bromate added in all years but 1942 and 1943, when $\frac{3}{4}$ per cent malted wheat flour was added.

The greatest number of tests were with Baart and Baart 38, and the greatest differences also were found between these paired varieties. Perhaps the most significant difference between Baart and Baart 38 is in their bread-making properties. Baart 38 has rather consistently produced lower loaf volumes, and grain, texture, and crumb-color values. These differences are small, but nevertheless appear to be significant, especially when considered in relation to the slightly higher protein content in Baart 38. Thus while it is not improbable that some other formula for making bread might make as good bread from Baart 38 as any shown here for Baart, Baart 38 apparently must be admitted to have slightly different quality attributes from Baart. This is further evidenced by the slight superiority of yellow loaf cake and of cookies baked from Baart 38. Other quality differences between Baart and Baart 38 shown in table 5 probably are not real. Many of the tests suggest close similarity rather than any difference between Baart and Baart 38.

Quality averages for three other backcross-derived varieties and their prototypes also are reported in table 5. For these, and for three other derivatives tested for only 1 year—Pacific Bluestem 37, Big Club 37, and Sonora 37—the data suggest general similarity in quality to their comparably grown prototypes. If some of the small differences are real, further testing will be necessary to establish the reality. In any case a fairly close approximation of the physical and chemical, as well as the baking responses of the prototype varieties obviously has been obtained by the backcross method of breeding as practiced in California.

DISCUSSION

From the data presented, critics of the backcross method can readily point to differences, and supporters even more readily to similarities. As the person who has been privileged to observe and study the performance of these varieties most extensively and intensively, the writer has sought to give this new breeding method a strictly objective evaluation.

In paired plantings, even a skilled agronomist usually cannot detect any morphological differences between the backcross-derived varieties and their prototypes, much less distinguish them. In rare instances, both can be done, usually by the manifestation of greater variability within the backcross-derived population. In this connection, it is important to recall that all of these varieties resulted from the making of a rather large number of crosses in each backcross generation and finally merging many F_3 or F_4 lines. It is this bulking of lines which probably accounts for the aggregate performance being so like that of the commercial variety under all environments, and yet makes possible minor aggregate differences in yield, test weight, plant height, and quality. That these or any other undetermined aggregate differences are more than minor differences certainly does not seem likely from the data at hand. Thus, there is justification for use of the common name, and general substitution of the backcross-improved stock wherever its imparted resistance is useful.

The variability occurring in the improved variety is both useful and dangerous. If a nonrecurrent parent in the pedigree of a backcross-derived variety possesses some desirable trait that has not been eliminated through conscious

selection, it can probably be recovered by extensive selection. The recent recovery of selections of Baart 38 with purple straw, light red seeds, and stripe-rust resistance, are indicative of the possibilities, as are the selections from Federation 41 that are superior in winter hardiness or mildew resistance.

The diversity occurring is desirable when a variety is being improved by a succession of backcrosses with different varieties. Independent advanced breeding programs underway in California anticipate production of: (1) awnless; (2) short-strawed; (3) early-maturing; and (4) bronze-glumed forms of Baart that are resistant to both smut and stem rust. Two further backcrosses to Baart recently have been made partly to utilize the maximum level of stem-rust resistance extant in Baart 38, but more especially to minimize the genetic diversity from Baart. This stock, to be known as Baart 46, may never be grown commercially but it will be used as the recurrent parent instead of Baart in concluding backcrosses for the production of the new types mentioned above and for other future crossing. Thus, while only five or six backcrosses were necessary to achieve the high similarities reported herein, two or more additional backcrosses seem desirable when more than three improvements are to be consolidated into one improved variety.

SUMMARY

The average yields of nine backcross-derived varieties grown in paired comparisons with their commercial prototypes in tests in nine western states failed to show any general significant differences in yield between the paired strains when disease and insect injury were absent or the same for both strains.

However, significant differences in yield were evident at two stations. At Tetonia, Idaho, there was an 11 per cent yield advantage for Baart as compared with Baart 38 and at Aberdeen, Idaho, Federation showed a 5 per cent advantage over Federation 41.

From an average of more than 60 tests, Baart 38 excelled in test weight by 0.33 pound and was 0.36 inch shorter than Baart. Though these differences have a high mathematical probability of being real, they represent differences of only 0.6 and 0.9 per cent, respectively. Baart 38 was inferior to Baart in bread-making quality.

All of the data emphasize the high degree of similarity between varieties and their progenies produced from five or more backcrosses. Substitution for existing commercial varieties of any of the improved varieties herein considered, or of any subsequently produced by similar successful breeding methods, seems desirable wherever the effected improvements will operate to minimize production losses. Except for the specified improvements, the general performance of the improved varieties has been indistinguishable from those of the progenitor varieties.

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